Mortality, growth and regeneration following fragmentation of reef-forming corals under thermal stress

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ABSTRACT

Storms inflict damage to corals resulting in fragments that have the potential to regenerate thus contributing to the asexual reproduction of the parental colony. Extreme climatic events like these are predicted to increase in the future due to ocean warming, which is also the primary cause of coral reef bleaching and consequent coral mortality in the tropical and subtropical seas. This way it is urgent to investigate the differential effect of warming over post-fragmentation and regeneration processes among the scleractinian hermatypic coral species. This study investigated the mortality, growth and regeneration capacity of nine reef-forming coral species of the Indo-Pacific. Fragments were exposed to 26 °C, 30 °C, and 32 °C for 60 days. Half of these fragments was inflicted with one injury and the other half was used as control. Mortality, partial mortality, bleaching level, growth and regeneration of artificial injuries were assessed. Mortality increased with temperature, reaching 100% for most species after 60 days, at 32 °C, but *Psammocora contigua* which showed remarkably lower mortality (40%) and all coral fragments of *Turbinaria reniformis* and *Galaxea fascicularis* survived the experiment. Partial mortality was lowest for *P. contigua*, *T. reniformis*, and *G. fascicularis* even at 32 °C. These three coral species were also the most resistant to bleaching. Growth rates decreased with temperature, with the exception of *G. fascicularis* that maintained similar growth rates at 26 °C and 30 °C. Regeneration rates generally increased with temperature. It was concluded that *P. contigua*, *T. reniformis*, and *G. fascicularis* fragments show higher capacity to withstand higher temperatures.

1. Introduction

Corals are dominant species of tropical coral reef ecosystems and have a unique and complex symbiotic relationship with dinoflagellate microalgae (zooxanthellae), contained within their gastrodermal cells (Hoegh-Guldberg, 1999). The ability of scleractinian corals to deposit calcium carbonate skeletons and to generate the physically complex reef structure is attributed to these dinoflagellates (Meehan & Ostrander, 1997).

Global climate change is leading to both rising sea surface temperatures and ocean acidification, jeopardizing coral reefs survival (Carpenter et al., 2008; Padilla-Gamiño et al., 2013). However, it has been shown by recent studies that the warming of tropical oceans is a much more imminent threat to coral reefs' survival than is ocean acidification (e.g., (Chua et al., 2013; Frieler et al., 2012)). The reef-building corals that undergo bleaching have reduced growth rates and reproductive capacity (Baird & Marshall, 2002; Szmant & Gassman,

1990), impaired healing (Meesters & Bak, 1993), and increased susceptibility to disease (Harvell et al., 1999). Bleaching makes the host organism white due to a loss of symbionts, which allows the underlying skeleton to be visible (Baker et al., 2008). If thermal stress is sustained, this may result in widespread coral mortality (Brown et al., 2002; Szmant & Gassman, 1990). Mass bleaching episodes have the potential to dramatically change coral community structure (Gleason, 1993; Glynn, 1993) and in severe cases cause population collapse and local extinction (Aronson et al., 2000).

An increase in the frequency and intensity of bleaching events is expected (Eakin et al., 2009; Heron et al., 2016), given that sea temperatures surrounding coral reefs are projected to increase by 1–3.7 °C by the year 2100 (IPCC, 2014). Globally, thermally induced bleaching due to climate change was predicted to occur annually in most oceans by 2040 (Crabbe, 2008; Hoegh-Guldberg, 1999; van Hooidonk & Huber, 2009). Associated with ongoing increases of tropical sea surface temperatures (SST) are increases in the frequency and maximum

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intensity of categories 4 and 5 storms (0–25%), and increases in tropical cyclones rainfall rates (5–20%) (Christensen et al., 2013; IPCC, 2014).

Due to wave action (Stimson, 1978), storm surge (Randall & Eldredge, 1977), and touristic activities (e.g. diving, snorkeling, and trampling; (Davenport & Davenport, 2006)) coral fragments may become detached from parent colonies and disperse across the reef (Highsmith, 1982). Increased storminess should favor the ability to propagate effectively by fragmentation (Lasker, 1990). Many branching corals are routinely broken and scattered about during storms (e.g., (Highsmith, 1980; Tunnicliffe, 1981)). Asexual reproduction by fragmentation of plating and massive coral forms has also been noticed (Foster et al., 2007).

Fragmentation of established colonies resulting in the formation of new coral colonies is known as an extremely important asexual mode of reproduction for many of the major reef-building corals (Bruno, 1998; Highsmith, 1982). Fragmentation by corals with high growth rates results in their domination of certain reef zones (Tunnicliffe, 1981), rapid growth of reefs on which these corals are abundant (Glynn et al., 1994), and rapid recovery from disturbances (Glynn & Fong, 2006; Shinn, 1976). Fragmentation may be adaptive (Cook, 1979; Highsmith, 1982; Highsmith et al., 1980), given that a considerable number of the most successful corals have incorporated fragmentation into their life histories. Asexual reproduction is probably the main process involved in the origin of new coral reefs (Glynn, 1993).

There is interspecific variability in reef-building corals' susceptibility to increased temperature (McClanahan et al., 2007; Seveso et al., 2014). Their susceptibility depends on colony morphotype (Brandt, 2009), tissue thickness (Loya et al., 2001), colony size (Shenkar et al., 2005), the capacity to transfer mass and heat (van Woesik & Jordán-Garza, 2011), coral species (Hoegh-Guldberg & Salvat, 1995; Marshall & Baird, 2000), genetic variation between coral populations from widely separated geographic regions (Coles et al., 1976; Glynn et al., 1988; Rowan & Knowlton, 1995), and the genetic constitution of the symbiotic microalgae (*Symbiodinium* spp.) (Rowan et al., 1997).

In many coral bleaching reports, there is noticeable variation in the extent of bleaching, as some colonies remain pigmented but adjacent ones of the same or different species undergo bleaching (Baker et al., 2008; Montano et al., 2010; Rowan et al., 1997). These different susceptibilities lead to major structural shifts in coral communities (Aronson et al., 2004; Ostrander et al., 2000), where hardier corals (i.e. massive and encrusting thick-tissued species) will eventually replace less resilient corals (i.e. branched and thin-tissued species) (Kayanne et al., 1999; van Woesik et al., 2011).

The aim of this work was to evaluate how elevated temperatures will affect the mortality, growth and regeneration after fragmentation of an important number of reef-building corals of the Indo-Pacific oceans. Such an evaluation is crucial to understand the differential vulnerability of reef-forming coral species to global climate change.

2. Material and methods

2.1. Study species

This study evaluated nine Indo-specific coral species with contrasting morphologies: four branching species (*Acropora tenuis, Pocillopora damicornis, Stylophora pistillata,* and *Psammocora contigua)*, three plating species, (*Montipora capricornis* brown morphotype (BM), *Turbinaria reniformis,* and *Echinopora lamellosa)*, one encrusting species (*Montipora capricornis* green morphotype (GM)), and one massive species (*Galaxea fascicularis)*. All coral colonies used in this study have been kept in captivity at Oceanário de Lisboa (Portugal) for several years, which gave us knowledge on their thermal history.

These coral species were chosen in order to use the largest number of species available at Oceanário de Lisboa with different levels of bleaching susceptibility: severe (*A. tenuis, P. damicornis,* and *S. pistillata*), high (*M. capricornis*), moderate (*E. lamellosa*), and low (*T.*

reniformis, G. fascicularis, and *P. contigua)* (Marshall & Baird, 2000), and different colony morphology, a characteristic that has been proven to have influence in coral species susceptibility to thermal stress (Loya et al., 2001). Coral species identification was made according to Veron (Veron, 2000).

2.2. Acclimation conditions and experimental setup

The experiments were conducted at Oceanário de Lisboa, Portugal (www.oceanario.pt).

Twenty replicate fragments were cut from each coral colony using a pincer or a pair of pliers. For the branching coral colonies the fragments were cut approximately 20–40 mm in length and the fragments for the plate, encrusting and massive corals were obtained by cutting approximately 30 mm sided squares. A single colony per coral species was targeted in order to eliminate sources of variation from other factors that affect thermal susceptibility (Desalvo et al., 2008) such as tissue thickness (Loya et al., 2001), genetic constitution of the symbiotic microalgae (*Symbiodinium* spp.) (Rowan et al., 1997), metabolic rates (Gates & Edmunds, 1999), mucus production rates (Fitt et al., 2009), tissue concentration of fluorescent pigments (Salih et al., 1998), and thermal history (Brown et al., 2002). All fragments were placed over egg crate panels in the coral stock aquarium until acclimation to the experimental aquarium.

The live wet mass of each coral fragment was obtained by blotting it with a paper towel to remove excess seawater, then weighing it in air on an electronic balance to the nearest 0.01 g (Titlyanov et al., 2005). Each fragment was glued with epoxy putty to the top of a pre-weighed and numbered nylon expansion anchor. Placement of the fragment varied by morphology with the branching fragments in vertical position and the plating, encrusting and massive fragments placed in horizontal positions. Then, the set (coral fragment + anchor) was weighed to remove the epoxy putty weight off the calculations and placed back over egg crate panels in the coral stock aquarium.

After one day in the coral stock aquarium, the sets were acclimated 1 °C per hour above the temperature of the coral stock aquarium (25.1 ± 0.4). Coral reef-flat communities can experience temperature changes of 1 °C hour^{-1} during spring tides (Berkelmans & Willis, 1999), and most of the coral species in this study colonize the reef-flat zone (Brown & Suharsono, 1990), so we used this heating rate to be similar to the conditions that most of these corals would experience in their natural environment. In order to standardize, this heating rate was applied for all the coral species. The coral fragments were placed 2 cm apart from one another and arranged by coral species. Fragments were exposed to three temperature treatments: control 26 °C (26.1 ± 0.2 SD), 30 °C (30.2 ± 0.5 SD) and 32 °C (32.2 ± 0.5 SD) seawater temperatures during sixty days, with the duration of one, five and seven hours of acclimation, respectively.

Ten coral fragments of each species were used as controls (undamaged) and the other ten fragments were inflicted with circular injuries designed to simulate damage by predators, after being acclimated to the experimental aquarium. These artificial injuries were 3 mm in diameter and were done using a Dremel rotatory tool with a cutting disk. Only one injury was inflicted to each coral fragment in their middle section to avoid edge effects (Supplementary material – Image 1). After these procedures, all fragments were placed over two 40 × 40 cm egg crate panels suspended 15 cm below the water surface of the experimental aquarium.

The experimental aquarium (400 L) was fitted with a sump (280 L) filled with bioballs for biological filtration in which two Fluval M300 heaters, as well as a Hailea 500 chiller controlled water temperature. For water circulation purposes, an AquaMedic OceanRunner 3500 pump provided a turnover rate of 5 times per hour. An AquaMedic Turboflotor 5000 Shorty protein skimmer helped keeping nutrient concentrations low and increased surface water motion in the aquarium was accomplished by using an AquaClear 110 powerhead. Lighting

Table 1

Summary of results of PERMANOVA permutation tests applied to report the effects of temperature, coral species and presence/absence of injury in coral fragments' mortality, partial mortality, growth and regeneration rates. Significant differences are marked a bold.

	df	SS	MS	Pseudo-F	p(perm)
Mortality					
Temperature	2	6.9×10^5	3.5×10^5	5.98×10^2	**0.0001**
Coral species	8	5.4×10^5	6.7×10^4	1.17×10^2	**0.0001**
Injury	1	3.9×10^2	3.9×10^2	0.67	0.5537
Temperature $\times$ Coral species	16	6.3×10^5	4.0×10^4	68.43	**0.0001**
Temperature $\times$ Injury	2	3.0×10^3	1.5×10^2	2.59	**0.0193**
Coral species $\times$ Injury	8	6.8×10^3	8.5×10^2	1.50	0.0749
Temperature $\times$ Coral species $\times$ Injury	16	2.6×10^4	1.6×10^3	2.85	**0.0001**
Partial mortality					
Temperature	2	6.6×10^5	3.3×10^5	4.80×10^2	**0.0001**
Coral species	8	5.3×10^5	6.6×10^4	96.10	**0.0001**
Injury	1	1.2×10^3	1.2×10^3	1.72	0.1610
Temperature $\times$ Coral species	16	5.7×10^5	3.6×10^4	51.93	**0.0001**
Temperature $\times$ Injury	2	1.9×10^3	9.5×10^2	1.37	0.2282
Coral species $\times$ Injury	8	6.3×10^3	7.9×10^2	1.14	0.2918
Temperature $\times$ Coral species $\times$ Injury	16	2.0×10^4	1.3×10^3	1.89	**0.0009**
Growth rate					
Temperature	2	26.0	13.0	3.21×10^2	**0.0001**
Coral species	8	25.0	3.1	77.35	**0.0001**
Injury	1	7.9×10^{-4}	7.9×10^{-4}	1.94×10^{-2}	0.8929
Temperature $\times$ Coral species	8	11.1	1.4	34.38	**0.0001**
Temperature $\times$ Injury	2	0.3	0.1	3.36	**0.0367**
Coral species $\times$ Injury	8	0.7	8.7×10^{-2}	2.15	**0.0307**
Temperature $\times$ Coral species $\times$ Injury	8	0.5	6.3×10^{-2}	1.56	0.1376
Regeneration rate					
Temperature	2	2.7	1.3	26.39	**0.0001**
Coral species	8	6.2	0.8	15.35	**0.0001**
Temperature $\times$ Coral species	16	4.1	0.3	5.08	**0.0001**

requirements similar to the coral stock aquarium were attained by using a Litpa Jet5 floodlight with an AquaMedic 400 W HQi lamp (13,000 K) on a 12 h light/ 12 h dark cycle. An air-stone was used in the aquarium to ensure good oxygen concentrations.

Photosynthetically Active Radiation (PAR) levels were measured with a spheric quantic sensor (LI-193SA) and a data logger (1400 model) and varied between 320 and 345 $\mu E.m^{-2} s^{-1}$ in the 400–700 nm waveband. Water quality parameters such as water temperature, pH and salinity were measured on a daily basis. Water samples were also weekly analyzed to determine ammonium, nitrites, nitrates, calcium concentration as well as oxygen concentration and saturation and alkalinity. These parameters were maintained as follow: pH at 8.2–8.3, salinity at 33–33.5 psu, alkalinity approximately at 100 $mg\, l^{-1}$, nitrites between 0.002 and 0.005 $mg\, l^{-1}$, nitrates between 0 and 2 $mg\, l^{-1}$, calcium concentration between 389 and 401 $mg\, l^{-1}$, oxygen saturation at 104% and oxygen concentration between 6.5 and 7.1 $mg\, l^{-1}$. Salinity was maintained with daily balanced additions of reverse osmosis freshwater and filtered artificial seawater. Whenever alkalinity levels were below 100 $mg\, l^{-1}$ sodium bicarbonate was added to the system. Aquarium cleaning routines were done as required to avoid algal growth, and these included expansion anchors cleaning with a toothbrush and egg crate replacement, at least 3 times a week.

2.3. Analytical procedures

2.3.1. Mortality assessments and bleaching level

Mortality was quantified as the percentage of dead fragments and partial mortality was visually quantified by estimating the percentage of dead area in the coral fragments and put it into four classes: [0,25%[, [25,50%[, [50,75%[and [75,100%]. The bleaching level of each coral species was visually assessed according to four categories: normal, pale, bleached and dead (Jokiel & Coles, 1974). Mortality and bleaching were assessed every 20 days until the end of the experiment and always by the same person to remove observer bias.

2.3.2. Growth rate measurements

The coral fragments were weighted both in the first and last day of the experiment in order to calculate the growth rates for each coral fragment. The growth rate of the coral fragments was calculated using the formula:

$$\mu = (m_1 - m_0/m_0 \times \Delta t) \times 100$$

where, μ is the growth rate measured in $g\, g^{-1}\, day^{-1}$, m_0 is initial weight, m_1 is the weight at the end of the experiment, and Δt is the time between the two measurements of weight (Brinkhuis, 1985).

2.3.3. Regeneration rate of injuries

The size of the injury was measured immediately after their infliction and then every 20 days until the end of the experiment. Injury recovery was quantified by recording the diameter of each injury with a steel caliper calibrated in millimeters. The tissue regeneration rates (Ts) were obtained by calculating, the difference between the areas of the recovered surfaces (Ra) for any given interval (T1 and T0 in days), as follows (Cróquer et al., 2002):

$$Ts = [Ra(T_1) - Ra(T_0)]/(T_1 - T_0)$$

2.4. Statistical analyses

A permutational multivariate analysis of variance (PERMANOVA) based on Euclidean distances (Anderson, 2001) was used to test whether coral fragments' mortality, partial mortality, growth and regeneration rates were affected by temperature and coral species. PERMANOVA was also used to test whether coral fragments' mortality, partial mortality and growth rate were affected by the presence/absence of injury. Values of the pseudo-F statistic were computed using 9999 permutations. Analyses were performed using PERMANOVA+ for PRIMER v6 (PRIMER-E Ltd., Plymouth). As PERMANOVA is based on permutations it is more robust to the assumptions of ANOVA (Anderson, 2001). Post-hoc pair-wise comparisons were then performed

using PERMANOVA to compare between temperature experiments and coral species. Differences were considered significant at $p < .05$.

3. Results

The presence/absence of injury had no effect on the mortality, partial mortality and growth rate of the fragment (PERMANOVA $p > .05$, Table 1) and therefore it was not considered as a factor in further analysis, with no separation between control and injured fragments.

3.1. Mortality and bleaching level

3.1.1. Mortality

Mortality was significantly affected by the independent effects of temperature and coral species (PERMANOVA $p < .05$, Table 1). There was also a significant effect of the interactions of temperature and coral species (PERMANOVA p $< .05$, Table 1).

Coral fragments' mortality presented significant differences among temperatures (PERMANOVA p $< .05$, Table 1), with the exception of *A. tenuis* fragments that showed similar mortality between 26 °C and 30 °C (PERMANOVA pair-wise $p > .05$, Fig. 1a).

The fragments of *A. tenuis* presented mortality at both 26 °C and 32 °C, however, at 26 °C they presented 10% mortality and maintained it stable until the end of the experiment (Fig. 1a). At 30 °C, *A. tenuis* did not show any mortality, whereas at 32 °C it perished on the 60th day (Fig. 1a).

Acropora tenuis, P. damicornis, and *S. pistillata* had significantly greater mortality since the 20th day (15% - 25%) than all other coral species at 32 °C (PERMANOVA pair-wise $p < .05$, Fig. 1), but did not vary among each other (PERMANOVA pair-wise $p > .05$, Fig. 1a, g and h).

3.1.2. Partial mortality

Partial mortality was significantly affected by the independent effects of temperature and coral species (PERMANOVA p $< .05$, Table 1). There was also a significant effect of the interactions of temperature and coral species (PERMANOVA p $< .05$, Table 1).

Coral fragments' partial mortality presented significant differences among temperatures (PERMANOVA p $< .05$, Table 1), with the exceptions of *A. tenuis* and *T. reniformis* fragments. *A. tenuis* showed similar partial mortality between 26 °C and 30 °C, whereas *T. reniformis* showed it among all temperatures (PERMANOVA pair-wise $p > .05$, Fig. 2a and d).

The fragments of *A. tenuis* presented partial mortality in the [75,100] class at both 26 °C and 32 °C, however, at 26 °C they presented very low percentage and maintained it stable until the end of the experiment (Fig. 2a). At 30 °C, *A. tenuis* only started to show partial mortality on the 40th day, whereas at 32 °C it started on the 20th day and with higher partial mortality (Fig. 2a).

Acropora tenuis, P. damicornis, and *S. pistillata* had significantly greater partial mortality since the 20th day (20% - 25% in the [75,100] class) than all other coral species at 32 °C (PERMANOVA pair-wise $p < .05$, Fig. 2), but did not vary among each other (PERMANOVA pair-wise $p > .05$, Fig. 2a, g and h).

Montipora capricornis (GM) and *E. lamellosa* fragments presented intermediate levels of partial mortality when compared with the other coral species in study (PERMANOVA pair-wise p $< .05$, Fig. 2), but did not vary among each other (PERMANOVA pair-wise $p > .05$, Fig. 2c and e). These coral species presented low percentage of partial mortality in the same class (5% and 30% in the [75,100] class on the 40th day for *M. capricornis* (GM) and *E. lamellosa*, respectively, Fig. 2c and e).

Turbinaria reniformis and *G. fascicularis* fragments had significantly less partial mortality than all other coral species at 32 °C (PERMANOVA pair-wise p $< .05$, Fig. 2), but did not vary between each other (PERMANOVA pair-wise $p > .05$, Fig. 2d and f). These coral species

presented low percentage of partial mortality in the same class (5% and 15% in the [25,50[class on the 60th day for *T. reniformis* and *G. fascicularis*, respectively, Fig. 2d and f).

3.1.3. Bleaching level

At 26 °C, almost all the coral species remained with their normal coloration throughout the 60 days experiment (Fig. 3). *A. tenuis* was the most sensitive species with 10% of their coral fragments dead by the 20th day of the experiment (Fig. 3a).

At 30 °C, the fragments of *A. tenuis*, *M. capricornis* (GM), *E. lamellosa*, and *G. fascicularis* remained normal throughout the experiment (Fig. 3a, c, e and f). Seventy five percent of the fragments of *M. capricornis* (BM) and *P. contigua* were pale on the 60th day of experiment, whereas the ones of *T. reniformis* were completely paled on the 40th day (Fig. 3b, d and i). A decrease in the percentage of bleached fragments was evident in *P. damicornis* and *S. pistillata* fragments since the 20th day (80% and 5%, respectively) due to them succumbing to mortality that reached the 100% on the 60th day of the experiment (Fig. 3g and h).

At 32 °C, the coral species *A. tenuis, M. capricornis* (BM)*, M. capricornis* (GM)*, E. lamellosa, P. damicornis, S. pistillata,* and *P. contigua* increased in the bleaching level since the 20th day, whereas the coral species *G. fascicularis* only presented it since the 40th day, with all these species reaching the dead level, exception for *G. fascicularis* (Fig. 3a-c and e-i). The coral species *T. reniformis* only reached the pale level (Fig. 3d).

3.2. Growth rate

In Table 2, not available (NA) indicates that the coral fragments of a specific coral species were dead before the end of a given temperature experiment.

Temperature significantly impacted growth rates (PERMANOVA $p < .05$, Table 1) with the highest growth rates of all coral species observed at 26 °C, except for *G. fascicularis*. This species growth rate was similar at 26 °C and 30 °C (PERMANOVA pair wise $p > .05$; Table 2). Each of the other coral species showed significant intraspecific differences among temperatures (PERMANOVA pair wise $p < .05$), with the exception of *P. contigua* that had its growth rate impacted in the same way at 30 °C and 32 °C (PERMANOVA pair wise p $> .05$; Table 2).

At 26 °C, *A. tenuis* and *P. contigua* had the highest growth rates (PERMANOVA pair wise $p < .05$) ($1.64 \pm 0.38 \, \text{g g}^{-1} \text{day}^{-1}$ and $1.54 \pm 0.32 \, \text{g g}^{-1} \text{day}^{-1}$, respectively; PERMANOVA pair wise $p > .05$), whereas *G. fascicularis* displayed the lowest growth rates ($0.28 \pm 0.08 \, \text{g g}^{-1} \text{day}^{-1}$, PERMANOVA pair wise $p < .05$; Table 2). At 30 °C, *A. tenuis* had the highest growth rates ($0.57 \pm 0.12 \, \text{g g}^{-1} \text{day}^{-1}$, PERMANOVA pair wise $p < .05$), whereas *E. lamellosa* and *M. capricornis* (GM) displayed the lowest growth rates (PERMANOVA pair wise $p < .05$) ($0.17 \pm 0.06 \, \text{g g}^{-1} \text{day}^{-1}$ and $0.14 \pm 0.05 \, \text{g g}^{-1} \text{day}^{-1}$, respectively; PERMANOVA pair wise p $> .05$; Table 2). At 32 °C, *P. contigua* had the highest growth rates ($0.42 \pm 0.10 \, \text{g g}^{-1} \text{day}^{-1}$, PERMANOVA pair wise $p < .05$), whereas *T. reniformis* displayed the lowest growth rates ($0.11 \pm 0.06 \, \text{g g}^{-1} \text{day}^{-1}$, PERMANOVA pair wise $p < .05$; Table 2).

3.3. Regeneration rate

In supplementary material 1, not available (NA) was used in the time points after regeneration of all the coral fragments for a given coral species and when the coral fragments died.

Regeneration rate was significantly affected by the independent effects of temperature and coral species (PERMANOVA $p < .05$, Table 1). There was also a significant effect of the interactions of temperature and coral species (PERMANOVA $p < .05$, Table 1).

Regeneration rates of *M. capricornis* (BM), *G. fascicularis*, and *P. contigua* increased from the 26 °C experiment (PERMANOVA pair wise
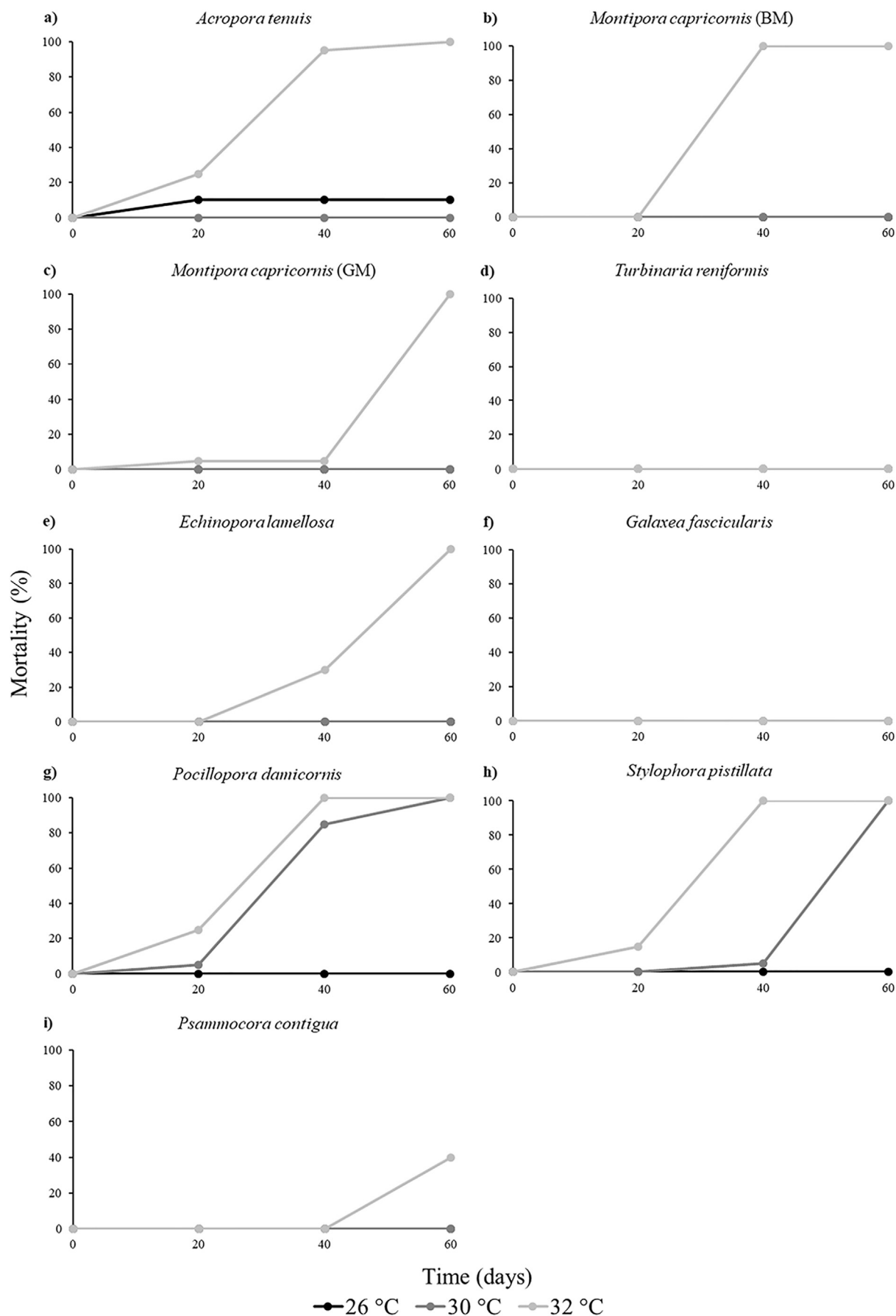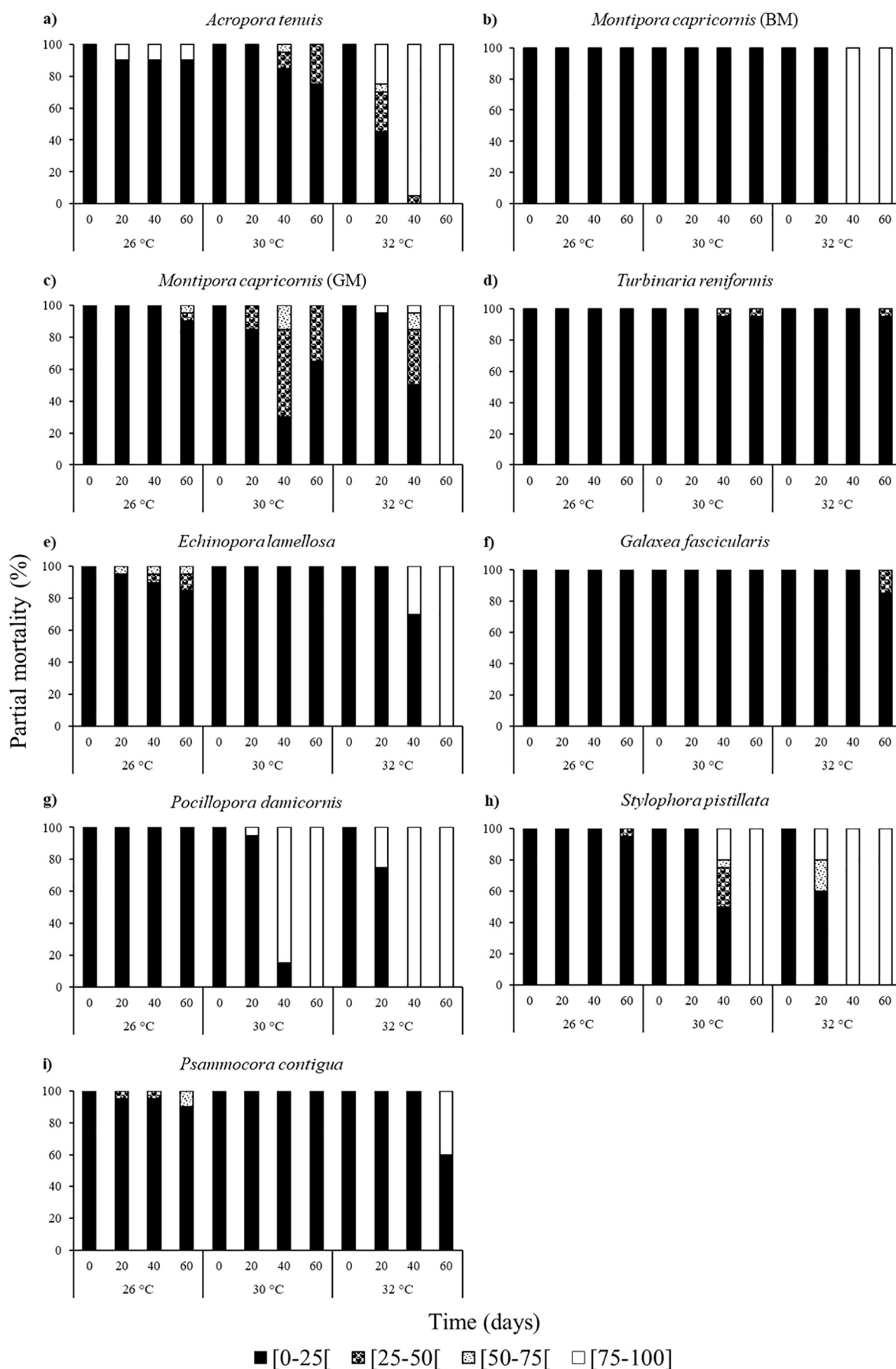
Fig. 1. Mortality of the coral species' fragments studied throughout the three temperature experiments.

Fig. 2. Partial mortality of the coral species' fragments studied throughout the three temperature experiments separated in percentage classes [0,25%[, [25,50%[, [50,75%[and [75,100%].
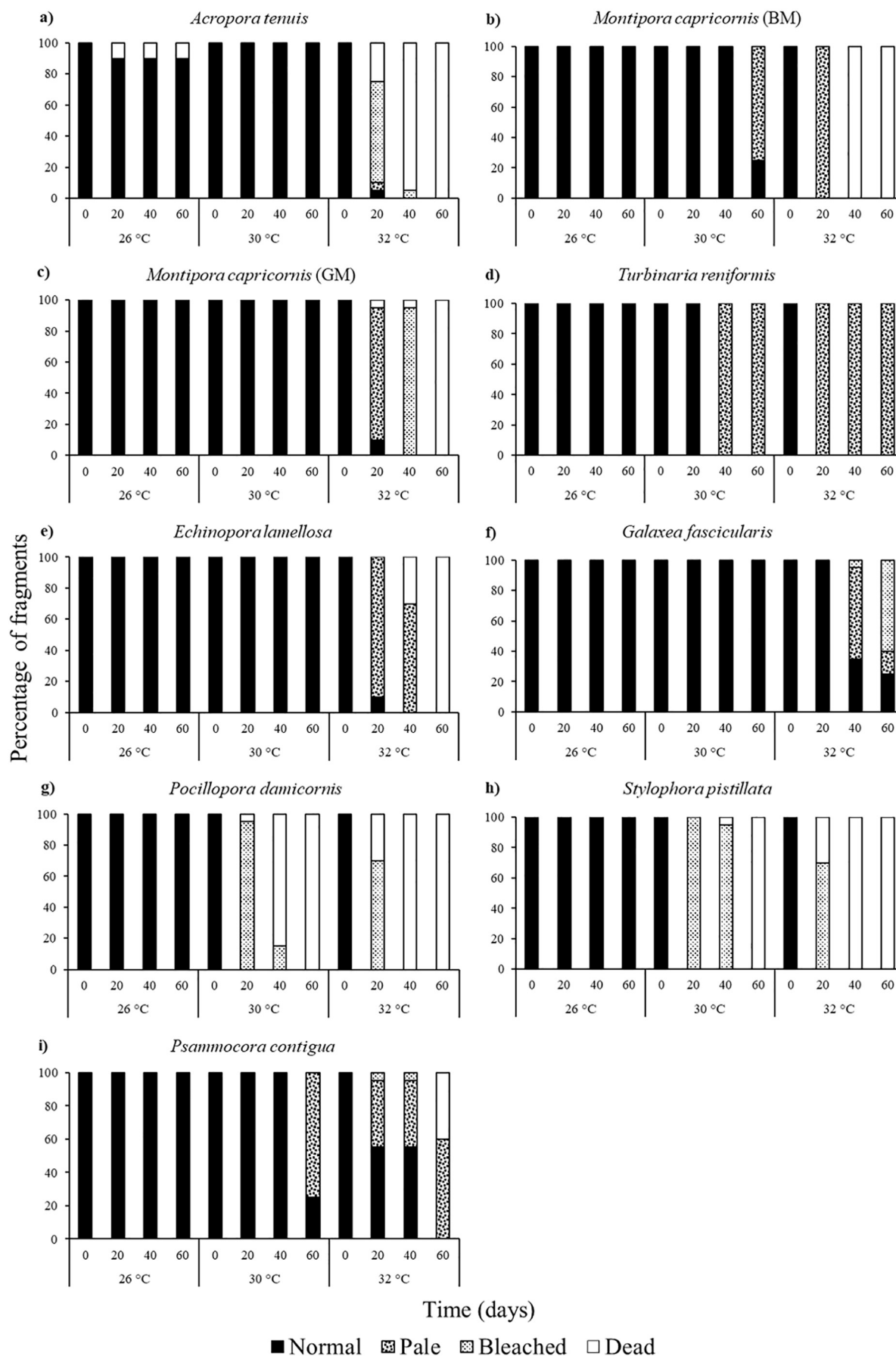
Fig. 3. Bleaching level of the coral species' fragments studied throughout the three temperature experiments.

Table 2

Coral fragments' average growth rate ± standard deviation in the three temperature experiments (g g^{-1} day^{-1}). NA – not available.

Species	26 °C	30 °C	32 °C
Acropora tenuis	1.64 ± 0.38	0.57 ± 0.12	NA
Montipora capricornis (BM)	0.92 ± 0.20	0.34 ± 0.21	NA
Montipora capricornis (GM)	0.79 ± 0.20	0.14 ± 0.05	NA
Turbinaria reniformis	0.56 ± 0.33	0.24 ± 0.09	0.11 ± 0.06
Echinopora lamellosa	0.51 ± 0.36	0.17 ± 0.06	NA
Galaxea fascicularis	0.28 ± 0.08	0.28 ± 0.10	0.20 ± 0.09
Pocillopora damicornis	1.23 ± 0.23	NA	NA
Stylophora pistillata	0.76 ± 0.19	NA	NA
Psammocora contigua	1.54 ± 0.32	0.41 ± 0.13	0.42 ± 0.10

Table 3

Coral fragments' average regeneration rate ± standard deviation in the three temperature experiments (mm^2 day^{-1}) measured until complete regeneration or the last time point they were still alive. For more information see Supplementary material – Table 1.

Species	26 °C	30 °C	32 °C
Acropora tenuis	0.23 ± 0.09	0.42 ± 0.22	0.30 ± 0.14
Montipora capricornis (BM)	0.24 ± 0.16	0.69 ± 0.21	0.51 ± 0.27
Montipora capricornis (GM)	0.17 ± 0.03	0.16 ± 0.07	0.09 ± 0.07
Turbinaria reniformis	0.16 ± 0.10	0.35 ± 0.16	0.52 ± 0.16
Echinopora lamellosa	0.30 ± 0.11	0.58 ± 0.27	0.84 ± 0.18
Galaxea fascicularis	0.30 ± 0.06	0.73 ± 0.27	0.88 ± 0.48
Pocillopora damicornis	0.40 ± 0.13	0.50 ± 0.25	0.13 ± 0.02
Stylophora pistillata	0.65 ± 0.29	0.71 ± 0.32	0.46 ± 0.13
Psammocora contigua	0.22 ± 0.10	0.59 ± 0.27	0.63 ± 0.49

$p < .05$, Table 3) to both 30 °C and 32 °C experiments (PERMANOVA pair wise $p > .05$, Table 3). *A. tenuis* regeneration rate only was significantly different between 26 °C and 30 °C, whereas *S. pistillata* showed it between 30 °C and 32 °C (PERMANOVA pair wise $p < .05$, Table 3). *T. reniformis* and *E. lamellosa* regeneration rates were significantly different among all temperature experiments (PERMANOVA pair wise p < .05, Table 3), both *M. capricornis* (GM) and *P. damicornis* regeneration rates decreased significantly at 32 °C (PERMANOVA pair wise p < .05, Table 3).

At 26 °C, the fragments of *S. pistillata* presented the highest regeneration rates (0.65 ± 0.29 mm^2 day^{-1}, PERMANOVA pair wise p < .05), whereas the lowest regeneration rate was presented by *M. capricornis* (BM), *T. reniformis,* and *M. capricornis* (GM) fragments (PERMANOVA pair wise p < .05) (0.24 ± 0.16 mm^2 day^{-1}, 0.16 ± 0.10 mm^2 day^{-1} and 0.17 ± 0.03 mm^2 day^{-1} respectively; PERMANOVA pair wise $p > .05$; Table 3). At 30 °C, *G. fascicularis*, *S. pistillata*, *M. capricornis* (BM), *P. contigua*, *E. lamellosa,* and *P. damicornis* had the highest regeneration rates (PERMANOVA pair wise p < .05) (0.73 ± 0.27 mm^2 day^{-1}, 0.71 ± 0.32 mm^2 day^{-1}, 0.69 ± 0.21 mm^2 day^{-1}, 0.59 ± 0.27 mm^2 day^{-1}, 0.58 ± 0.27 mm^2 day^{-1}, 0.50 ± 0.25 mm^2 day^{-1} respectively; PERMANOVA pair wise p > .05), whereas *M. capricornis* (GM) displayed the lowest regeneration rates (0.16 ± 0.07 mm^2 day^{-1}, PERMANOVA pair wise p < .05, Table 3). At 32 °C, the fragments of *E. lamellosa*, *G. fascicularis*, and *P. contigua* had the highest regeneration rates (PERMANOVA pair wise p < .05) (0.84 ± 0.18 mm^2 day^{-1}, 0.88 ± 0.48 mm^2 day^{-1} and 0.63 ± 0.49 mm^2 day^{-1}, respectively; PERMANOVA pair wise p > .05, Table 3), whereas *P. damicornis* and *M. capricornis* (GM) displayed the lowest regeneration rates (PERMANOVA pair wise p < .05) (0.13 ± 0.02 mm^2 day^{-1} and 0.09 ± 0.07 mm^2 day^{-1}, respectively; PERMANOVA pair wise p > .05, Table 3).

4. Discussion

Acropora tenuis, P. damicornis, and *S. pistillata* had the highest

susceptibility to thermal stress during the study, displaying more bleaching and tissue loss early in the experiment compared to other species. In field studies, branching acroporids (e.g. *Acropora* spp.) and pocilloporids (e.g. *Pocillopora damicornis* and *Stylophora pistillata)* are the taxa most sensitive to bleaching stress, usually suffering high mortality, particularly in the Indo-Pacific (Fujioka, 1999; Marshall & Baird, 2000). *T. reniformis* only presented partial mortality by the 40th day at 30 °C and at the end of the 32 °C experiment, and both *G. fascicularis* and *P. contigua* only presented it at the end of the 32 °C experiment, indicating that these coral species fragments are most resistant to thermal stress than the other coral species fragments in study. In the field, *Turbinaria*, *Galaxea*, and *Psammocora* are considered resistant to bleaching displaying low mortality when compared with other taxa, with their unbleached colonies generally surrounded by bleached colonies of other taxa (Bhagooli & Hidaka, 2003; Marshall & Baird, 2000; Stimson et al., 2002).

The discoloration evidenced by the corals in this study resulted from either the loss of their zooxanthellae, the degradation of their photosynthetic pigments, or a combination of both, with the extent of their bleaching and ultimately their mortality possibly being considered as good stress indicators (Glynn, 1993; Hoegh-Guldberg, 1999). At 30 °C, the coral species *M. capricornis* (BM), *T. reniformis,* and *P. contigua* showed color attenuation although never reaching the bleached level, whereas *P. damicornis* and *S. pistillata* reached the bleached level and complete mortality. These findings make us consider that *M. capricornis* (BM), *T. reniformis,* and *P. contigua* fragments probably presented higher levels of stress at 30 °C than at 26 °C, displayed as color attenuation at 30 °C, and that *P. damicornis* and *S. pistillata* are highly susceptible to thermal stress since they were the only ones with bleached fragments and complete mortality at 30 °C over the course of 60 days. At 32 °C, most of the coral species died, except for *T. reniformis, G. fascicularis,* and *P. contigua,* however, the time interval in which they reached complete mortality varied interspecifically. *T. reniformis* and *G. fascicularis* showed no mortality throughout all the experiment and only 40% of *P. contigua* fragments were dead at the end of this experiment. These findings make us consider these three species as highly tolerant to thermal stress due to their null or low mortality over the course of 60 days. The bleaching level of all coral species was highest at 32 °C. This can be explained by the higher thermal stress present at higher temperatures (Glynn, 1984; Goreau et al., 2000).

The hierarchy of species susceptibility to thermal stress presented here: (*A. tenuis, P. damicornis*, *S. pistillata*) > *M. capricornis* (BM) > (*M. capricornis* (GM), *E. lamellosa)* > *P. contigua* > (*T. reniformis, G. fascicularis*) is in accordance to the ones observed in other studies with species of the Indo-Pacific (Marshall & Baird, 2000; Stimson et al., 2002).

According to our results, coral survival declined significantly at 32 °C with an increase in bleaching level and mortality with increasing exposure, although it had remained high at 26 °C and 30 °C. A probable explanation could be related to corals' bleaching temperature threshold, which in many regions is close to 31 °C (Glynn, 1984; Goreau et al., 2000), thus confirming the high bleaching level and mortality observed at 32 °C. Our results are also in accordance with those of Stimson et al. (Stimson et al., 2002) who reported high mortalities for *Acropora* spp., *Pocillopora damicornis,* and *Stylophora pistillata* and low mortalities for *Turbinaria* spp., *Galaxea fascicularis*, and *Psammocora contigua* during the bleaching event of late summer 1998 in northern Okinawa.

At 32 °C, *G. fascicularis* fragments acquired a lighter coloration than their typical red-brown coloration. This discoloration was most obvious on the coenosarc between the corallites, while individual polyps remained with their red-brown coloration. In these flat surfaces of tissue, the algae are likely to experience the cumulative effects of highest light intensities and elevated temperature, while the algae situated in the base of a polyp or in the tentacles might experience shading by the coral's tissue and skeleton or other algae (Brown et al., 1995). In the last twenty days of this experiment, the fragments of *G. fascicularis* changed

to white with yellow fluorescent polyps possibly due to the presence of fluorescent pigments in the coral that enhanced its bleaching resistance (Salih et al., 2000).

Our results show that the cause of bleaching in these coral species might probably be an interaction between water temperature and the amount of time above their bleaching threshold, rather than just having temperatures above their bleaching threshold (Fitt et al., 2001; McClanahan et al., 2001). In particular, there was a pronounced difference among these coral species in the time necessary to respond to thermal stress. The most likely explanation for this phenomenon is the existence of differences in interspecific respiration rates. Faster-growing species, such as the *Acropora spp.*, are generally assumed to have a higher respiration rate than the slower-growing massives, and a high correlation between respiration rate and coral susceptibility to thermal stress has long been recognized (Gates & Edmunds, 1999; Jokiel & Coles, 1990).

Another explanation for the time taken for the different coral species in this study to respond to thermal stress might be related with the fact that colony morphology also influences coral vulnerability to bleaching. Branching pocilloporids *(Stylophora pistillata, Pocillopora damicornis)* and staghorn corals *(Acropora spp.)* are cited in many studies, both in experimental work (Jokiel & Coles, 1974) and in bleaching episodes in the field (Glynn, 1983; Loya et al., 2001), as being morphologies severely damaged by thermal stress (Brown & Howard, 1985; Hoegh-Guldberg & Salvat, 1995). These corals bleach more often than massive and encrusting growth forms (Loya et al., 2001; Marshall & Baird, 2000; McClanahan et al., 2002). However, other factors must also be considered such as tissue thickness (Loya et al., 2001), density of zooxanthellae or the weight of tissue per unit coral surface area (Stimson et al., 2002), the clade of *Symbiodinium* spp. (Magalon et al., 2007), taxa or coral phylogeny (McClanahan et al., 2004), density of fluorescent tissue pigment granules (FPG; (Salih et al., 2000)), and colony integration (Baird & Marshall, 2002). Previous studies have identified *Turbinaria reniformis, Galaxea fascicularis,* and *Psammacora contigua* as tolerant species to thermal stress (Marshall & Baird, 2000; Yamazato, 1981; Yamazato, 1999), which the results of this study support. Although *P. contigua* has branching morphology, it was reported to have high densities of zooxanthellae in comparison with the densities of other branching genera such as *Pocillopora, Acropora, Stylophora* (Stimson et al., 2002).

Growth rate has been cited as one of the best quantitative measures to test stress due to a disturbance, since this parameter integrates a variety of physiological processes (Birkeland et al., 1976; Muscatine, 1990; Pratchett et al., 2015). In the fragments of acroporid species (*Acropora tenuis* and *Montipora capricornis*) it was possible to observe the spread of the basal tissue over the epoxy putty or the bare skeleton following its contour, known as fast self-attachment after transplantation (Guest et al., 2011), whereas in the fragments of *T. reniformis, E. lamellosa,* and *G. fascicularis* no self-attachment was observed, as their growth occurred by horizontal extension of its margins. Also, the growing of several new branches in the fragments of *S. pistillata* was observed. This may happen as a way of *S. pistillata* to re-acquire the colony symmetry lost after its separation, which is a known characteristic of this species' colonies (Rinkevich, 2000).

According to our results, coral fragments' growth rates decreased with increasing temperature, which is in accordance with physiological data showing an accentuated decline in coral growth at temperatures only a few degrees above optimum levels (Berkelmans & Willis, 1999). In all temperature experiments, *A. tenuis* and *P. contigua* presented the highest growth rates, with the exception of *A. tenuis* at 32 °C that died. Assuming that plate and massive morphologies grow slower than branched ones (Guest et al., 2011), the lower growth rates of *G. fascicularis* at 26 °C, *M. capricornis* (GM) and *E. lamellosa* at 30 °C and *T. reniformis* at 32 °C can thus be justified. *G. fascicularis* was the only coral species that did not present significant growth rate differences at 26 °C and 30 °C, suggesting that this coral species is resistant to thermal

stress. All the other species presented significant differences at 26 °C and 30 °C, this probably is a result of thermal stress at 30 °C, where their growth rates were lower (Fine et al., 2002; Szmant & Gassman, 1990). The fragments of *P. contigua* did not present significant differences at 30 °C and 32 °C, which means that although this coral species had shown severe visual signs of stress at 32 °C, its growth rate was affected in the same way at these temperatures.

The ability of corals to regenerate from injuries is crucial to their survival from disturbances such as hurricanes and predators since poor regenerative ability can lead to a reduction in colony fitness (Hall, 1997). Coral fragments' regeneration rate differed with temperature. The coral species *A. tenuis, M. capricornis* (BM), *T. reniformis, E. lamellosa, G. fascicularis,* and *P. contigua* seem to benefit with the increase in temperature as their regeneration rates increased with temperature, thus confirming the assumption that an increase in water temperatures accelerates coral fragments' metabolism and, as long as their specific stress levels were not attained, their regeneration rates will be greater at higher temperatures (Coles & Jokiel, 1977; Kramarsky-Winter & Loya, 2000). Having this in mind, the coral species *M. capricornis* (GM), *P. damicornis,* and *S. pistillata* might have presented their highest stress levels at 32 °C where they showed their lowest regeneration rates.

Hall (Hall, 1997) ranked the regenerative ability of eleven different coral species according to their morphologies (arborescent > bushy > tabular > massive > submassive). Our study results were not in accordance with those of Hall (Hall, 1997), probably because the experimental conditions were different. Hall's work was developed in natural environment whereas ours was developed in laboratory. In natural conditions, corals are exposed not only to changes of other environmental variables (e.g. salinity (Faxneld et al., 2010), solar radiation (Lesser & Farrell, 2004), sedimentation and turbidity (Browne, 2012), aerial exposure (Teixeira et al., 2013), water flow (Lenihan et al., 2008)), but also to competition (Baird & Hughes, 2000), predation (Rotjan & Lewis, 2008), algal over growth (Diaz-Pulido et al., 2009), and continuous colony overturning (Campbell et al., 2007), which in the present study were controlled. Also, the fact that in this study we used small fragments instead of large colonies, the use of different coral species, the ratio diameter of injury/coral area was much higher than the one used in this study, and Hall (Hall, 1997) made observations for a longer period of time which would allow for more healing time of the injured corals (74 days instead of 60 days). All these factors are known to affect corals' regeneration capacity of lesions (Denis et al., 2011).

Differential susceptibility and mortality among species can exert a major influence on coral community structure (Pratchett, 2001). According with the results obtained in this study, it is expected that the coral species *T. reniformis, G. fascicularis,* and *P. contigua* will be more resistant to high temperature and bleaching episodes and thus becoming more important in terms of coral cover. Nevertheless, it is important to have in consideration that the more fragile and thermal susceptible coral species tend to be fast-growing species (Marshall & Baird, 2000; McClanahan et al., 2004) and that in some bleaching episodes it has been observed that more resistant coral species did not increase in absolute density and cover through time because they are often slow-growing species (Guest et al., 2016; van Woesik et al., 2011).

On the other hand, other disturbances present in their natural habitat need to be taken into account, such as predation (Pratchett, 2001), competition (Baird & Hughes, 2000) and extreme events (e.g. tropical cyclones; (Fabricius et al., 2008)) that, like bleaching episodes, affect with greater magnitude fast-growing coral species. As a result, mortality of thermal susceptible species, often numerically dominant, may promote the coexistence of a higher number of species unless the increase in frequency of bleaching episodes causes local eradication or prevents susceptible species from resettle (Loya et al., 2001; McClanahan & Maina, 2003). Thus, although *T. reniformis* and *G. fascicularis* are slow-growing coral species, it is expected that these resistant species will become dominant. Although *P. contigua* is a fast-

growing coral species, it showed a high ability to resist to thermal stress and it is expected to increase in coral cover and subsequent dominance faster than *T. reniformis* and *G. fascicularis*. This pattern of recovery was observed in other studies (Baird & Marshall, 2002; Brown & Suharsono, 1990).

Another aspect to have into account is the ability of corals to adapt to recurrent thermal stress, which occurs through the selective removal of highly susceptible genotypes, followed by reproduction and successful recruitment of corals with higher photoprotective defense (influx of coral colonies with thermal tolerance) (Penin et al., 2013; Pratchett et al., 2013). It was observed in several studies that such adaptation may result in a reverse of the normal hierarchy of bleaching susceptible coral species (Carroll et al., 2017; Guest et al., 2016). Nevertheless, gradual adaptation to increased temperatures by coral assemblages in the Indo-Pacific can easily be undone, delayed or even stopped by other natural and anthropogenic stressors and disturbances (e.g. *Acanthaster planci* outbreaks; (Adjeroud et al., 2005)) and may have altogether different selective forcing on coral population and communities (Pratchett et al., 2013).

Having in account that this study was made with colonies coming from the same mother colony, meaning low genetic variability, it is important to consider that some results may vary with those in future studies.

In conclusion, long-term exposure to 32 °C was beyond the bleaching resistance capacity of the majority of the corals. *A. tenuis, P. damicornis*, and *S. pistillata* were the most affected by thermal stress, which may result in these species becoming less important in terms of coral cover in coral reef communities subjected to successive bleaching episodes, whereas the coral species *T. reniformis, G. fascicularis*, and *P. contigua,* due to their greater ability to resist to successive bleaching episodes as to other natural and anthropogenic stressors and disturbances, are likely to show greater capacity to withstand higher temperatures and might thus become more important in terms of coral cover. Nevertheless, *P. contigua* may increase in coral cover and subsequent dominance faster than *T. reniformis* and *G. fascicularis*. This knowledge may have ecological implications in coral reef conservation and management, as well as in the understanding of coral reef alterations in the near future.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2018.08.008.

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